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Population characteristics of the gastropod *Cantharidus pulcherrimus* on intertidal platforms in the Perth area of Western Australia

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ABSTRACT

The trochid gastropod *Cantharidus pulcherrimus* is shown to be abundant on intertidal rock platforms in the Perth metropolitan area of Western Australia, where it is concentrated in the *Sargassum* algal zone. In this zone *C. pulcherrimus* is found living on macroalgae rather than the underlying rock. Density of snails varies seasonally, with maximum density occurring in summer and minimum density in autumn. Recruitment of juveniles into the population occurs during the winter (June-August). The young snails grow rapidly and spawn at one year of age in March or April. A small proportion of the adults survives for a second year. Loss of snails as macroalgae are washed from the platform by winter storms is the largest known source of mortality. The life history strategy of *C. pulcherrimus* is discussed in relation to that of other trochids.

INTRODUCTION

The shoreline along the Perth metropolitan area of the central west coast of Western Australia is dominated by extensive sand beaches interrupted by small beachrock platforms. The platforms vary in tidal height, but most are at an intertidal level of about 0.4m in an area where the maximum tide range is about 1m. The geology of the platforms was described by Fairbridge (1950) and Semeniuk and Johnson (1985). The latter authors distinguished four types of platforms depending on the inshore structure of the platform and sandy beach. While the inshore structures vary in their characteristics the platforms themselves are more uniform. They are usually flat, often with a seaward rim which traps water on the platform surface at low tide. Solution pipes, channels and crevices make the surface irregular. The platforms generally extend from a landward cliff, which may have a sandy beach at its base, seaward for distances of a few to 100m. At the seaward margin the platform drops off sharply into a subtidal cliff which extends to the bottom, usually sand, in a few metres of water. The platforms are thus discrete habitats.

The central west coast of Western Australia is a faunal overlap zone with a mixture of three faunal elements: tropical Indo-West Pacific species extending down from the north coast; southern Australian temperate species ranging up from the south coast; and a small (< 10%) group of species endemic to Western Australia (Wilson and Gillett, 1971; Wells, 1980). Platforms along the western end of Rottnest I., 20km offshore from Perth, have a substantial proportion of tropical species. Tropical species are less numerous on platforms along the metropolitan coastline. Those which occur are generally uncommon and contribute little to the total density and biomass of molluscs; molluscs of the metropolitan platforms are virtually all temperate species (Wells, 1985).

In the mid 1960s a commercial fishery was started along the central west coast of Western Australia for the abalone *Haliotis roei* Gray, 1827. A substantial portion of the catch comes from metropolitan platforms. Initially the fishery was divided into discrete commercial and amateur segments. Professional fishermen were permitted to fish only on the subtidal cliffs. While amateurs could also fish in this area most chose to collect abalone on the intertidal platform surface. As abalone populations declined on the platform surface in the early 1980s amateur fishermen began actively fishing on the subtidal cliffs, affecting the commercial fishery. At the same time other species of molluscs, particularly gastropods, were being fished by amateurs but little was known of the extent of the fishing or the species involved. A three year program was initiated in late 1982 with the objective of developing information on platform molluscs, particularly abalone (Wells and Keesing, in prep a; in prep b), for use by fisheries managers. Because of the possibility of using seasonal closures of the platforms as a management technique several studies of the reproductive seasonality and/or seasonal changes in the population structure of platform species were begun.

Trochid gastropods are diverse on the platforms, with nine species having been recorded, several of which reach high population densities. Little is known of the reproductive strategies of Australian trochids except for the work of Moorhouse (1932) and Underwood (1974). *Cantharidus pulcherrimus* (Wood, 1828), a temperate species, was selected for examination because it is the dominant gastropod in some areas of the platforms, reaching a maximum density of almost $500.m^{-2}$; only mytilid mussels in beds had higher recorded densities. Because of heavy swell conditions during winter, which make the subtidal cliffs inaccessible, the present study was conducted entirely on the platform surface.

MATERIALS AND METHODS

Three platforms were selected for this study: Waterman, Trigg I. and Cottesloe. Each platform was divided into habitats based on the types of macroalgae present. At Waterman and Trigg I. there were three algal zones: a seaward bare zone largely devoid of macroalgae; an intermediate *Sargassum* zone; and a shoreward inshore platform of mixed macroalgae. The platform at Cottesloe lacks a bare zone but has a broad *Sargassum* zone, the inshore portion of which was sampled in the present study.

To examine horizontal distributions on the platform transects were run across the platform at Trigg I. beginning at the seaward edge of the platform, running through the bare zone and the *Sargassum* zone and into the inshore platform area. Two transects were made on 23 and 25 April 1984 and six months later on 19 and 21 October 1984. There were 10 to 20 stations on each transect spaced at intervals of 2m. At each station the number of *C. pulcherrimus* on *Sargassum*, on other algae and on the platform surface were counted in a quadrat of 50cm x 50cm. The number of *Sargassum* holdfasts was counted and each measured to the nearest 1cm and the percentage of algal cover determined for *Sargassum* and total algae. Algal cover was estimated by using a quadrat $0.25m^2$ divided into a grid of 7 x 7 giving 49 intersections. Presence or absence of algae was recorded for each intersection.

To sample annual fluctuations in density of *C. pulcherrimus* samples were conducted in January from 1983 to 1986. A series of eight stations was established in the inshore platform and *Sargassum* zone on each platform. Stations were 5 to 10m apart depending on the extent of the habitat. At each station the number of *C. pulcherrimus* in each of four 0.25m^2 quadrats was counted and density calculated; data were then pooled. The inshore platform on each reef was sampled at quarterly intervals from January 1983 to January 1985 to examine seasonal density variations. The *Sargassum* zone is too rough to be quantitatively sampled in winter and was not studied.

To examine size-frequency characteristics *C. pulcherrimus* were collected at approximately monthly intervals at Trigg I., Waterman and Cottesloe from January 1984 to December 1985. In most months 300 individuals were measured but in some cases fewer snails were available. *Sargassum* was collected from the centre of each platform and placed in labelled calico bags. In the laboratory the *Sargassum* and inside of the bag were washed in freshwater to remove the snails, which were preserved in 10% formalin. Total shell length was measured to the nearest 1mm with calipers.

RESULTS

A general trend of low density of *C. pulcherrimus* in the bare zone, high densities in the *Sargassum* zone and low densities in the inshore platform at Trigg I. was found in both April and October. *C. pulcherrimus* had mean densities of less than 2.m^{-2} in the bare zone (Table 1). The density was nil in the inshore platform in April but 50.m^{-2} in October. Mean algal cover on the inshore platform was 0 ± 0% in April, but increased to 56 ± 9% in October. Density was greatest in the *Sargassum* zone both during the April (41.3/m^{-2}) and October (170.5/m^{-2}) samples. There was not a statistically significant difference between density of *C. pulcherrimus* in the bare zone and inshore platform in either April or October (t-test, $P > 0.05$), but the differences between densities in the *Sargassum* zone and both the inshore platform and bare zones were highly significant in both sampling periods (t-test, $P < 0.05$).

C. pulcherrimus is thus clearly concentrated in the *Sargassum* zone. The data collected can be used to determine where the animals occurred in this habitat (Table 2). In both April and October less than 4% of the *C. pulcherrimus* in the *Sargassum* zone were on the bare rock surface; over 96% of the individuals were on algae. In April 91% of the *C. pulcherrimus* were on *Sargassum* but in October only 54% were on *Sargassum* and 43% were on other algae. This suggests that the density of *C. pulcherrimus* in the *Sargassum* zone might be related to either the percent cover of *Sargassum* or of total algae. Table 3 represents the results of linear correlations between density of *C. pulcherrimus* and both percent *Sargassum* cover and percent total algal cover for April and October. r values ranged from 0.58 to 0.69. There was a statistically significant correlation between density of *C. pulcherrimus* and abundance of both *Sargassum* and total algae in both April and October (t-test. $P < 0.05$) (Table 3).

In addition to the change of the population of *C. pulcherrimus* in the different algal zones there are substantial seasonal and annual variations in the density of the species. Seasonal densities fluctuated considerably (Figure 1). The maximum reached was 134m^{-2} at Cottesloe in January 1983. The species was absent on the inshore platform at Waterman in April 1984, when it was completely covered by sand, and there were other occasions when densities were near zero. There is clear evidence of seasonality on all three platforms. In both years the maximum density occurred during January. Numbers declined during the winter to near zero before increasing in spring as recruits entered the population.

Substantial year to year fluctuations in the density of *C. pulcherrimus* were found on all the platforms (Figure 2). The only consistent pattern was that densities were substantially higher in the *Sargassum* zone than on the inshore platform. Annual variations in the two zones of one platform were generally similar, but there were differences between platforms. At Cottesloe densities were high in both zones in 1983, declined to lower levels in 1984, and then stabilized. A similar pattern occurred on the inshore platform at Waterman, but in the *Sargassum* zone density increased by an order of magnitude from 1983 to 1985 before declining in 1986. Density at Trigg I. declined in 1984, rose in 1985 and decreased in 1986.

The size frequency histograms for *C. pulcherrimus* (Figures 3, 4 and 5) show that at the beginning of sampling in January 1984 the population at Cottesloe was unimodal with most of the animals being 6 or 7mm in shell length. At Trigg I. and Waterman the population had greater size variabilities with most animals being 5 to 10mm long. By April 1984 the graphs for all three reefs were clearly unimodal, composed of adult individuals 6-12mm long. A small proportion (2%) of the population at Trigg I. and Waterman consisted of juveniles 2mm long. In June the size frequency histogram for Cottesloe changed substantially with recruitment of juveniles 0-2mm long into the population. These animals constituted 71% of the population in June. By July they were predominately 1-3mm long and the adults had disappeared. The main settlement period at Trigg I. and Waterman started a month later, with a substantial portion of the population on both reefs being small juveniles in July. By August virtually all of the population was young of the year at Trigg I. but some individuals of the 1983 year class survived at Waterman at least until November 1984. The populations of *C. pulcherrimus* at Waterman and Cottesloe continued to grow through the summer months. The population at Trigg I. was bimodal in January 1985, either due to a late settlement in 1984 or a sampling artefact, but graphs for subsequent months were unimodal.

There were a few small individuals in the population at Waterman and Trigg I. in March 1985 but these had disappeared by April. The 1985 recruitment began in June and continued until September. By December the 1985 young had grown to a mean size of 4.4mm. Recruitment at Trigg I. began a month later (July) and at Waterman it commenced in August.

Figures 6, 7 and 8 show the mean size of the various year classes of *C. pulcherrimus* over the two year period of January 1984 to December 1985 on the three platforms. Only means of year classes with more than 25 individuals in a given month are shown. At the beginning of sampling in January 1984 the populations were composed entirely of large individuals spawned in the autumn of 1983. Mean sizes ranged from 6.4mm at Trigg I. to 8.0mm at Waterman. By February the animals had reached nearly their maximum mean size and growth had slowed to near zero. The 1983 year class remained detectable in the populations for varying periods — until June 1984 at Cottesloe and September at Trigg I. At Waterman the 1983 group was still present in February 1985 and had a mean size of 10.5mm. In March 1985 the individuals spawned in 1983 were indistinguishable from the 1984 animals.

The 1984 year class appeared in the populations in June and July. The clearest growth data are from Cottesloe, where juveniles had a mean length of 1.3mm in June 1984 and grew rapidly to 7.1mm in February 1985, then slowed so the animals reached 8.5mm by August. While the data for Trigg I. are not as clear they show a rapid growth of the 1984 class during the spring and summer months with growth tapering off in the autumn as the animals reached adult size and presumably energy was channelled into gamete production. The 1984 year class fluctuated in mean size on the three platforms after about March 1985. The 1985 year class began to be distinguishable in June at Cottesloe, July at Trigg I. and August at Waterman. While the Waterman recruitment was the latest of the three platforms the animals were first detected at a mean size of 3.2mm, suggesting recruitment had actually been earlier. If the lines of growth are extrapolated back to an initial size of 0.0mm an estimate of the spawning season can be obtained. The mean size of the early months of each year class for Waterman fluctuated too much to obtain a reliable estimate. If the Cottesloe and Trigg I. data are used an estimate can be obtained that reproduction must have occurred in March/April.

If the graphs for the three platforms are superimposed it can be seen that the populations of *C. pulcherrimus* on the three platforms share basic features. Reproduction occurs in March/April of each year. Growth of juveniles is rapid through the next year until a mean size of 8 to 10mm is reached in March, when the animals are about a year old. After spawning the adults persist as a declining proportion of the population for several months until late winter. Within this general pattern there are important, consistent differences between Cottesloe and Waterman with Trigg I. being intermediate. The maximum mean size obtained by the 1983 and 1984 year classes at Cottesloe were 8.5mm. Animals at Trigg I. and Waterman were larger, reaching mean sizes of up to 10.0mm. The previous year class disappeared completely at Cottesloe in both 1984 and 1985, but at Waterman in both years some adults remained in the population until they became indistinguishable from the previous year class.

TABLE 1. Comparison of densities of *Cantharidus pulcherrimus* in three habitat zones on the platform at Trigg I.

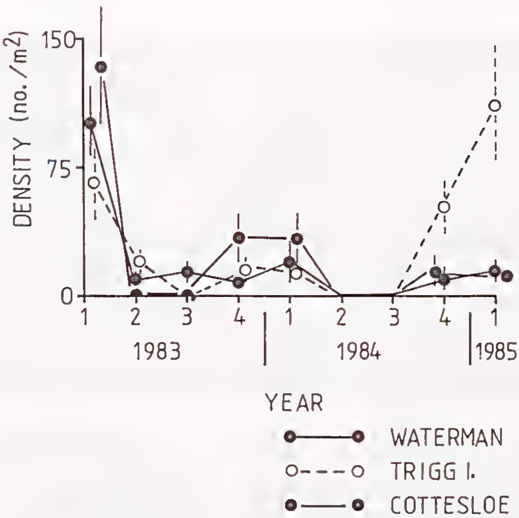
Zone	23-25 April 1984 No. stn.	Density of *C. pulcherrimus* (No. m^{-2} + 1 S.E.)	19-21 October 1984 No. stn.	Density of *C. pulcherrimus* (No. m^{-2} + 1 S.E.)
Bare zone	5	0.8 + 0.8	5	1.7 + 1.2
Sargassum zone	16	41.3 + 13.6	8	170.5 + 24.5
Inshore platform	4	0 + 0	21	50.5 + 11.9

TABLE 2. Comparison of densities of *Cantharidus pulcherrimus* on *Sargassum*, on other algae and on rock in the *Sargassum* zone of the platform at Trigg I.

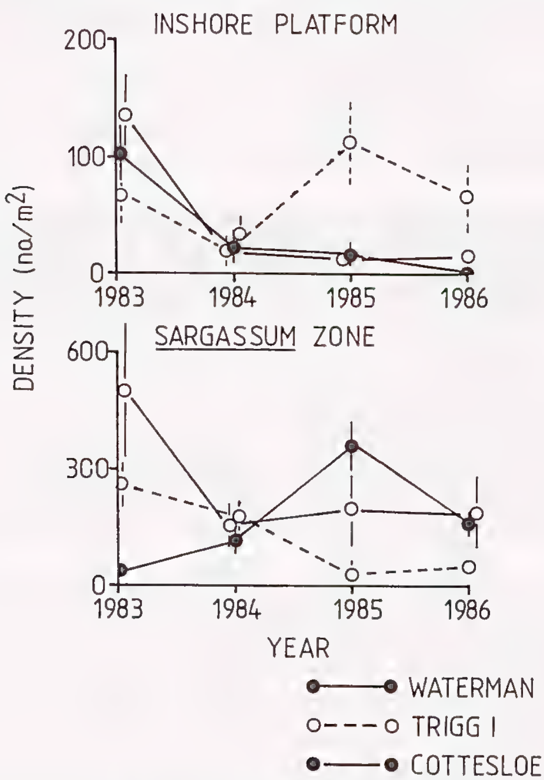
	23-25 April 1984 Density of *C. pulcherrimus* (No. m^{-2} ± 1 S.E.)	Algal cover (% ± 1 S.E.)	19-21 October 1984 Density of *C. pulcherrimus* (No .m^{-2} ± 1 S.E.)	Algal cover (% ± 1 S.E.)
On *Sargassum*	37.8 ± 13.1	31.5 ± 7.2	91.5 ± 18.6	54.4 ± 7.9
On other algae	2.3 ± 1.3	13.1 ± 4.2	73.0 ± 13.9	33.7 ± 6.9
On rock	1.2 ± 0.9		6.0 ± 2.6	
Total	41.3 + 13.6		170.5 + 24.5	

TABLE 3. Linear correlation between density of *Cantharidus pulcherrimus* and percent cover of *Sargassum* and total algae in the *Sargassum* zone on the intertidal platform at Trigg I. in 1984. The correlation is presented in the equation $Y = a + b X$ where Y is the density of *C. pulcherrimus*, a and b are constants and X is the percent algal cover.

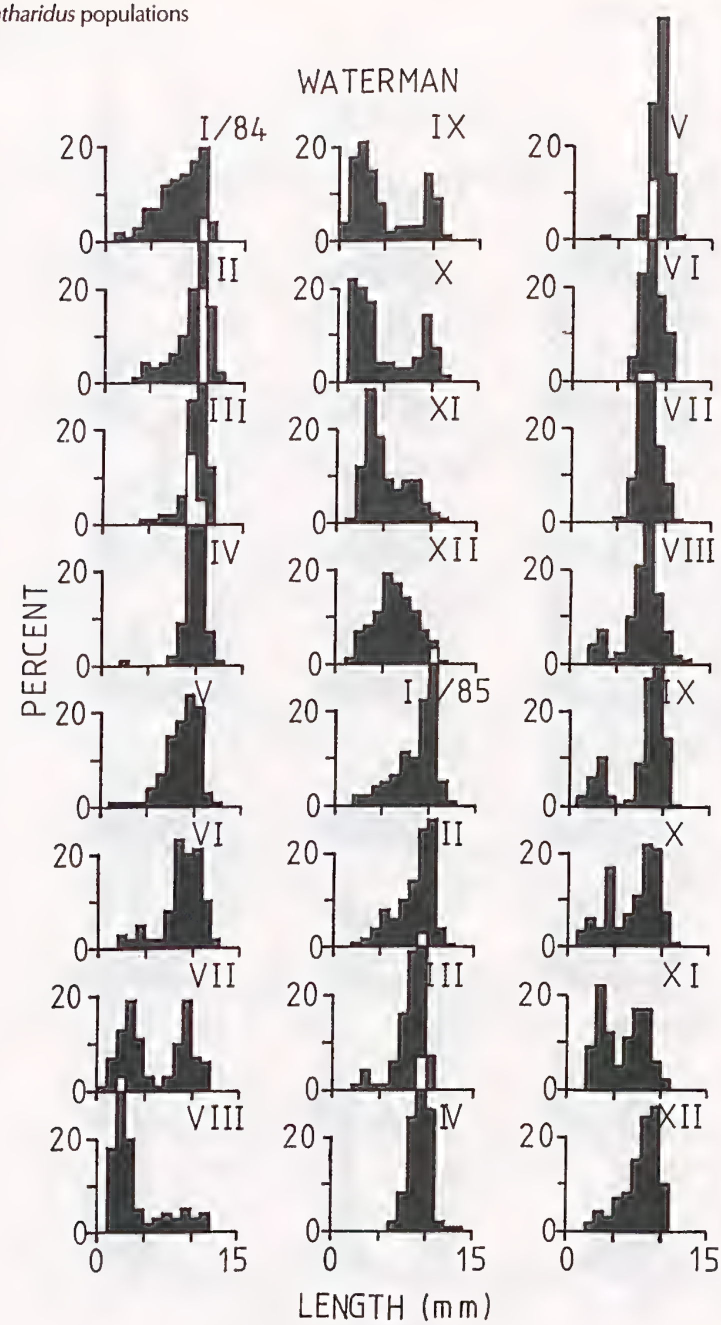
	a	b	r	r^2	Significance (t-test, 0.05 level)
April					
Sargassum	-0.58	1.29	.6927	.4799	*
Total algae	-7.49	1.09	.5795	.3358	*
October					
Sargassum	58.79	2.05	.6591	.4344	*
Total algae	-370.86	6.06	.6360	.4045	*



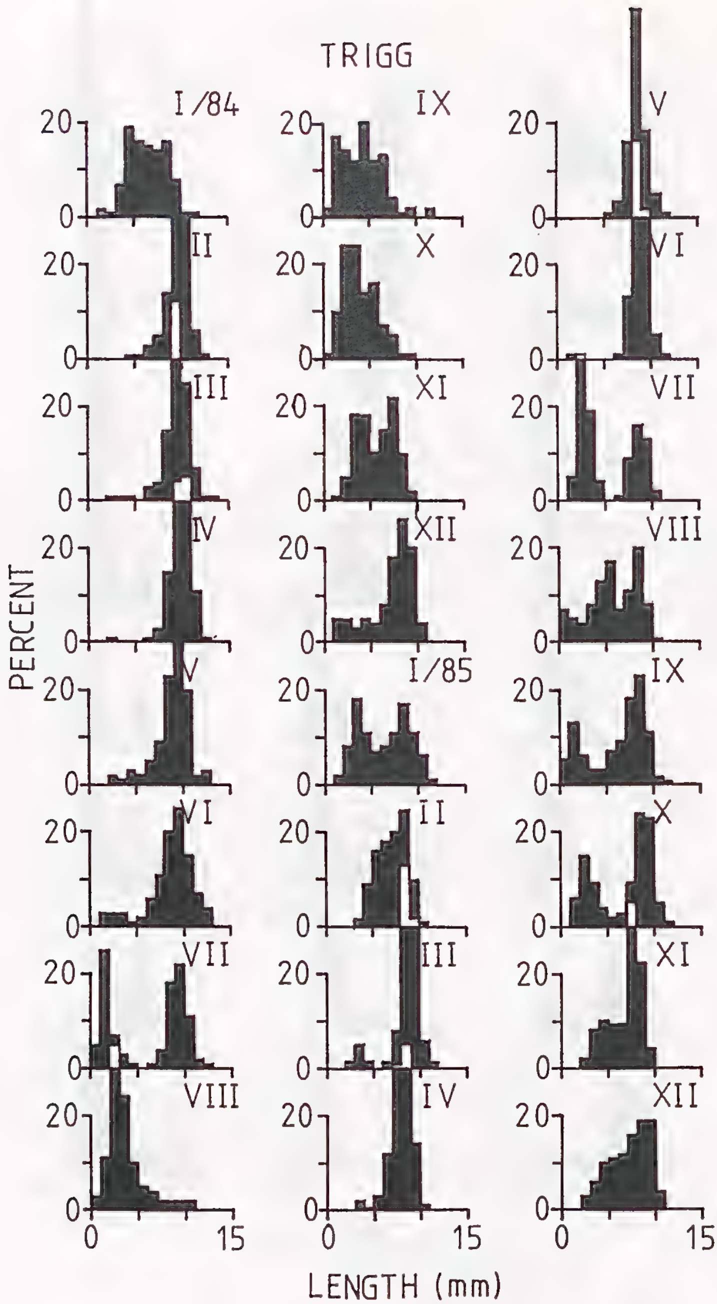
1. Seasonal variations in density of *Cantharidus pulcherrimus* on the inshore platform of three intertidal platforms in the Perth metropolitan area. Means and one standard error are shown.



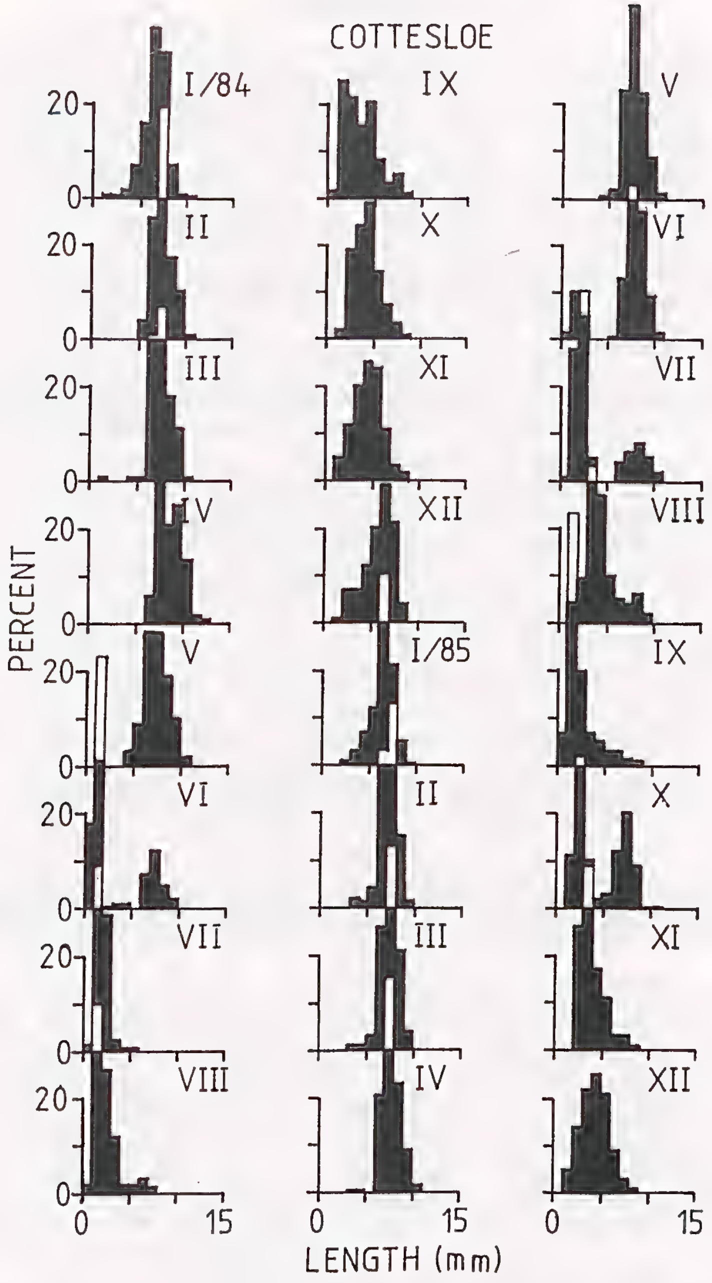
2. Annual variations in summer density of *Cantharidus pulcherrimus* in the *Sargassum* zone and on the inshore platform of three intertidal platforms in the Perth metropolitan area. Means and one standard error are shown.



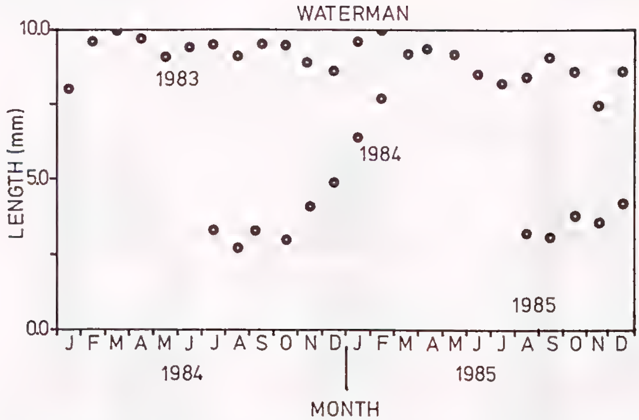
3. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Waterman at monthly intervals from January 1984 to December 1985.



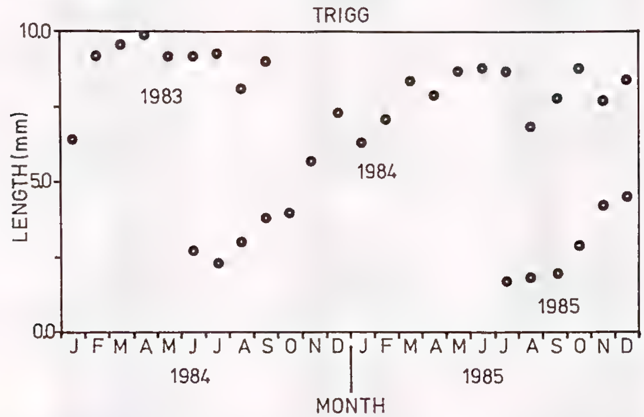
4. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Trigg I. at monthly intervals from January 1984 to December 1985.



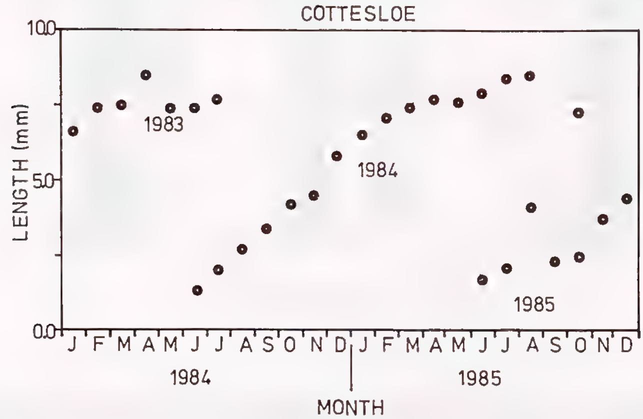
5. Size frequency characteristics of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Cottesloe at monthly intervals from January 1984 to December 1985.



6. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Waterman at monthly intervals from January 1984 to December 1985.



7. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Trigg I. at monthly intervals from January 1984 to December 1985.



8. Mean size of year groups of *Cantharidus pulcherrimus* collected in the *Sargassum* zone of the intertidal platform at Cottesloe at monthly intervals from January 1984 to December 1985.

DISCUSSION

Most archaeogastropods are dioecious and lack a penis. They are broadcast spawners, males and females both expelling gametes into the surrounding water column where fertilization takes place. After brief planktonic trochophore and veliger stages the young settle to the bottom to begin their juvenile life (Webber, 1977). The family Trochidae has hundreds of species (Abbott and Dance, 1982) but the reproductive strategies of only about a dozen have been studied. Some of the species examined are broadcast spawners with a planktonic veliger stage (Desai, 1966; Paine, 1971; Webber, 1977; Heslinga, 1981; Joska and Branch, 1983) but other species deposit benthic egg masses from which the young hatch as crawling young (Anderson, 1960; Duch, 1969). Even in species which undergo their entire larval development in the water column the planktonic stage is short, on the order of a week or less (Desai, 1966; Heslinga, 1981; Joska and Branch, 1983). The reproductive strategy of *C. pulcherrimus* was not studied. If the species has a veliger stage, as many of the previously studied trochids do, it would allow the repopulation of platforms by veligers spawned on adjacent platforms. Both young and adult *C. pulcherrimus* congregate on benthic macroalgae, particularly *Sargassum.* The macroalgae are easily dislodged by waves and swell, providing a second mechanism for dispersal of snails over the relatively short distances from one platform to another.

As with the reproductive strategy, reproductive periodicity has been studied for few species of trochids. Most of the temperate species examined have a single discrete spawning season which may last for several months (Paine, 1971; Underwood, 1972). *Oxystele variegata* (Anton, 1838) in South Africa has two distinct spawning seasons, February and September/October (Joska and Branch, 1983). While many tropical molluscs spawn year round the tropical trochids studied, *Tegula excavata* (Lamarck, 1822) in Barbados (Lewis, 1960) and *Euchelus gemmatus* (Gould, 1841) in Hawaii (Duch, 1969), both have restricted breeding seasons. The temperate species *Austrocochlea constricta* (Lamarck, 1822) studied in Sydney (Underwood, 1974) and the subantarctic *Cantharidus coruscans* (Hedley) (Simpson, 1977) are the only trochids known to spawn throughout the year. *C. pulcherrimus,* with a discrete spawning period in March/April thus fits into the general trochid pattern. Variation in the spawning periodicity of *Monodonta lineata* (Da Costa, 1778) in England has been found at different localities and in different years (Desai, 1966), paralleling the differences found between different platforms (particularly Cottesloe and Waterman) and between 1984 and 1985 for *C. pulcherrimus.* The extreme case reported was the failure of *Gibbula cineraria* (Linnaeus, 1758) to spawn in 1970 at Plymouth, England (Underwood, 1972). Such reproductive failure did not occur in *C. pulcherrimus* during the study period.

There are few data available on the lifespans of trochids. McQuaid (1982) showed that *O. variegata* in South Africa reaches a size of 14mm in one year, 18mm in two, and a proportion of the population was thought to survive beyond two years. *Tegula funebralis* (A. Adams, 1855) in Washington live up to 32 years (Paine, 1971).

Causes of mortality have not been directly investigated in *C. pulcherrimus,* but several can be discussed. Tides in the Perth area are small, with a maximum range of 1m, but there is a seasonal variation in sea level of about 0.3m (Hodgkin and Di Lollo, 1958). During winter the prevailing southwesterly or southerly airflow tends to be onshore and increases sea level. In summer the prevailing winds are offshore, decreasing tidal levels. Summer is also the season when easterly airflow generated by atmospheric high pressure systems may persist for several days, tending to keep water off the platforms. Air temperatures are high, up to 40°C or more, resulting in massive mortalities on the platforms (Hodgkin, 1959). Substantial decreases in the density of *C. pulcherrimus* possibly from high temperatures were recorded between January and April in both 1984 and 1985. However, *C. pulcherrimus* survived a bout of high temperatures in October 1985 when massive mortalities occurred amongst other molluscs (pers. obs.).

A second potential cause of mortality is the postreproductive death of adults. Such mortality has been suggested for *Nodilittorina unifasciata* (Gray, 1827) on the cliffs shoreward of the platforms at Waterman. *N. unifasciata* suffered substantial mortality during summer. As the summer conditions took the highest toll of adults it was considered to be postreproductive mortality (Wells, 1984). Declines in the population of *C. pulcherrimus* on the platform occurred between January and April, before the spawning season of *C. pulcherrimus,* suggesting that the cause was not postreproductive deaths of adult individuals.

Macroalgae on the platforms are seasonal, growing rapidly and being most diverse in summer. The macroalga *Ecklonia radiata* occurs on the platforms, particularly Cottesloe, but has been studied in subtidal locations. The greatest loss of *E. radiata* is during the heavy swell conditions of the winter months (Kirkman, 1981). *Sargassum* and other macroalgal populations on the platforms are substantially reduced by autumn and winter storms and thrown upon the beach in extensive drift beds (Lenanton, Robertson and Hansen, 1982). As the macroalgae are torn off the platforms most of the attached snails will be washed upon the beach and die, a major source of mortality for *C. pulcherrimus* since it lives on macroalgae rather than the underlying rock.

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